RESEARCH ARTICLE

Comparing Maternal Styles in Bonobos (*Pan paniscus*) and Chimpanzees (*Pan troglodytes*)

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Studies on *Cercopithecine* primate maternal styles, using factor analysis on a set of maternal behaviors, commonly render two factors that describe separate dimensions of maternal behavior: protectiveness and rejection. The aims of this study were to 1) investigate whether this method for determining maternal styles in *Cercopithecine* species can be applied to bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*), 2) determine whether they follow the same pattern, and 3) assess whether species differences in maternal style are apparent. We performed a factor analysis on nine maternal behaviors using data on eight mother–infant pairs of each species. This resulted in three factors: protectiveness, distance, and refusal. Protectiveness is positively correlated with time spent in ventral contact, making contact, approaching, and restraining. Distance is positively related with breaking contact and leaving. Refusal is positively correlated with rejecting and nipple-rejecting. The pattern of protectiveness corresponds with the pattern found in *Cercopithecine* species, suggesting a high consistency of this dimension across species and higher taxa. The retention of the other two factors indicates that in the *Pan* species, breaking contact and leaving represent another dimension, apart from rejecting and nipple-rejecting, which usually fall under one dimension in *Cercopithecine* species. An interspecific comparison of the factor scores for each dimension of maternal behavior reveals that, on average, bonobos and chimpanzees score equally on protectiveness. Scores on distance increase positively with infant age in chimpanzees, and negatively in bonobos, and on average bonobos have higher scores on refusal. These interspecies differences in maternal style are discussed in the light of interspecies differences in infant development, infant vulnerability to aggression, interbirth intervals, and female sociality. Am. J. Primatol. 64:411–423   © 2004 Wiley-Liss, Inc.

Key words: bonobo; chimpanzee; maternal style; interspecies differences

INTRODUCTION

Although mother–infant relationships have been intensively studied in a number of primate species over the last few decades [e.g., Altmann, 1980; Bentley-Condit & Smith, 1998; Berman, 1980, 1984, 1990; Hinde & Spencer-Booth, 1971; Horvat & Kraemer, 1981; Silk & Kraemer, 1978; van Lawick-Goodall, 1971], cross-species studies investigating the interaction between species-typical social organization and maternal behavior, and, more particularly, maternal style are scarce [Maestripieri, 1994a, b; Thierry, 1985].

Most studies on primate maternal styles have been conducted with *Cercopithecine* species in which variation in infant-directed behaviors usually falls along two dimensions: protectiveness and rejection [Bardi et al., 2001; Bardi & Huffman, 2002; Fairbanks, 1996; Fairbanks & McGuire, 1987, 1988]. Protectiveness is highly positively correlated with contact-making, approaching, restraining, and grooming the infant. Rejection is highly positively correlated with breaking contact, leaving, and rejecting the infant. These two dimensions or factors are not opposite ends of the same continuum, but vary independently from one another [Bardi et al., 2001; Bardi & Huffman, 2002; Fairbanks, 1996; Fairbanks & McGuire, 1988]. There appears to be a high degree of consistency in these basic dimensions of maternal behavior [Bardi et al., 2001; Bardi & Huffman, 2002; Fairbanks, 1996; Fairbanks & McGuire, 1988], which makes cross-species comparisons (at least between *Cercopithecine* species) feasible.

Our aims were to investigate whether a factor analysis to determine maternal style [Bardi et al., 2001; Bardi & Huffman, 2002; Fairbanks, 1996; Fairbanks & McGuire, 1988] could be applied to the two species of the genus *Pan* (bonobo (*Pan paniscus*) and chimpanzee (*Pan troglodytes*)), and to assess whether the outcome follows the *Cercopithecine* pattern. At the same time, we examined whether an interspecific difference in maternal style is apparent.

For years, the differences between bonobos and chimpanzees have been stressed. Presumably, typical bonobo characteristics, such as female dominance [Parish, 1994], highly promiscuous sexual interactions [de Waal, 1987; Kano, 1992], low levels of aggression [de Waal, 1998; Kuroda, 1980], higher reconciliatory tendencies [de Waal, 1998], and the apparent absence of infanticide [de Waal, 1998; Kano, 1998], contrast markedly with chimpanzee features. However, given the accumulating evidence of considerable overlap in the adaptive potential of bonobo and chimpanzee behavior [Doran et al., 2002; Stanford, 1998], the bonobo–chimpanzee dichotomy is being reconsidered [Fruth et al., 1999; Doran et al., 2002; Hohmann & Fruth, 2002; Vervaecke et al., 2003a]. Nevertheless, specific traits are apparent that still distinguish bonobos from chimpanzees [Doran et al., 2002]. These traits include 1) nonexclusive female dominance [Stevens et al., 2001; Vervaecke et al., 2000] and a greater tendency for bonobo females to possess and be responsible for distributing resources [Fruth & Hohmann, 2002], 2) greater female sociality [White, 1996], 3) few constraints from males against female aggressive behavior and severe female-initiated attacks toward males [Hohmann, 2001; Parish, 1996; Vervaecke et al., 2000, 2003b] (M.D.L., personal observation), and 4) no indications or evidence (to date) of infanticide performed by adult bonobo males.

Stumptail (*Macaca arctoides*), rhesus (*M. mulatta*), and pigtail (*M. nemestrina*) macaques, species that are characterized by important differences

in social and agonistic behavior [de Waal & Luttrell, 1989; Thierry, 1990], have been shown to differ in maternal style [Maestripieri, 1994b]. These documented differences represent adaptive responses to characteristics of the social environment, especially regarding the nature of infant-handling in these species [Maestripieri, 1994b]. Hence, given the important differences in social and agonistic behavior between the *Pan* species, a direct interspecies comparison could provide important information on the relationship between their social organization and maternal behavior.

MATERIALS AND METHODS

Data Collection

The subjects of this study were eight mother–infant pairs from each species, living in seven zoos (Table I). The sample included five female and three male infants of each species. Infant age ranged from 5–56 months in bonobos, and 7–47 months in chimpanzees. Maternal age ranged from 10 to 39 years in bonobos, and from 12 to 37 years in chimpanzees. Focal animal sampling on mother–infant dyads was conducted between January 2000 and December 2002 (for details, see PhD dissertation, De Lathouwers, 2004). Each mother–infant pair was sampled on average over five periods in 3 years. On average, the observation periods consisted of 6 consecutive days. Each day, five 30-min sessions were carried out randomly, resulting in 2.5 hr of observation a day and 15 hr per period. In total, 1,090 hr of data were collected.

All mother–infant pairs were socially housed in multimale/multifemale social groups that included animals of different age classes (except for the mother–infant pairs kept at Frankfurt Zoo, where group composition changed due to fission-fusion management). The bonobo group sizes ranged from eight to 12 individuals, and the chimpanzee group sizes ranged from 12 to 34 individuals. Given that our study was conducted during the course of 3 years, the group compositions inevitably changed due to natural dynamics (Table II).

We used the following behavioral measures of mother–infant interactions:

1. Time spent in ventral contact: proportion of the observed contact time that the infant spent in ventral contact with the mother.

2. Making contact: the number of movements made by the mother that resulted in any bodily contact between mother and infant relative to the total number of contacts made by mother and infant [Hinde & Atkinson, 1970].

3. Breaking contact: the number of movements made by the mother that broke any bodily contact, relative to the total number of contacts broken by mother and infant [Hinde & Atkinson, 1970].

4. Approaching: the number of movements made by the mother that reduced the distance between mother and infant relative to the total number of approaches made by mother and infant [Hinde & Atkinson, 1970]. We used three distance categories: within arm's reach, out of arm's reach but within 5 m, and >5 m. All distance changes that resulted in a lower distance category were considered as "approaching."

5. Leaving: the number of movements made by the mother that increased the distance between mother and infant, relative to the total number of leaves made by mother and infant [Hinde & Atkinson, 1970]. We used three distance categories: within arm's reach, out of arm's reach but within 5 m, and >5 m. All distance changes that resulted in a higher distance category were considered as "leaving."

TABLE I. Mother Infant Pairs

Mother	Date of birth	Age mother (yr)	Infant-sex	Date of birth	Infant age (mo)	Institution[b]
Pan paniscus						
Jill	15/7/1985	15–16	Tarishi-M	17/9/1998	16, 28, 32, 36	Apenheul
Molaso	1986[a]	14–16	Kumbuka-F	9/7/1999	6, 18, 22, 26	Apenheul
Zuani	1990[a]	10–13	Liboso-F	17/1/1998	24, 36, 40, 44, 56	Apenheul
Salonga	2/5/1973	27–29	Ferry-F	25/9/1999	5, 17, 21, 26	Frankfurt
Natalie	1/1/1963	39	Heri-M	23/3/2001	5, 10	Frankfurt
Hermien	1978[a]	22–25	Zomi-F	28/1/1998	23, 27, 32, 35, 39, 43, 55	Planckendael
Hortense	1978[a]	22–25	Zamba-M	16/4/1998	21, 25, 29, 33, 36, 41, 52	Planckendael
Lisala	24/4/1980	20–23	Opala-F	8/4/1998	23, 35, 39, 43, 54	Wuppertal
Pan troglodytes						
Sjors	1966[a]	34–37	Glafula-F	27/4/1999	9, 21, 25, 30, 41	Amersfoort
Nicole	20/10/1987	12–15	Dwangko-M	22/4/1999	9, 21, 25, 29, 41	Amersfoort
Silvia	1974[a]	27–29	Karibuna-M	24/10/2000	7, 11, 23	Amersfoort
Amber	17/7/1968	32–34	Allity-F	27/12/1998	14, 26, 30, 34, 47	Burgers' Zoo
Gaby	28/1/1984	16–19	Galatea-F	24/2/1999	12, 24, 28, 32, 45	Burgers' Zoo
Zaira	15/11/1983	16–19	Zwala-F	16/4/1999	10, 22, 26, 30, 43	Burgers' Zoo
Roosje	23/4/1979	22–24	Raimee-F	15/5/1999	21, 25, 29, 42	Burgers' Zoo
Lucy	11/11/1976	23–26	Liberius-M	20/1/1999	14, 26, 30, 34, 47	Edinburgh

[a]Estimated date of birth. Lisala (1), one infant was taken from the mother shortly after birth for hand- rearing; Silvia (1), one infant was taken from the mother around 2 years of age and transferred to another Zoo.
[b]Primate Park Apenheul, Apeldoorn, The Netherlands; Zoo Frankfurt, Frankfurt am Main, Germany; Wild Animal Park Planckendael, Mechelen, Belgium; Wuppertal Zoo, Elberfeld- Wuppertal, Germany, Animal Park Amersfoort, Amersfoort, The Netherlands; Edinburgh Zoo, Edinburgh, United Kingdom; Burgers' Zoo, Arnhem, The Netherlands.

TABLE II. Sex and Age Distribution of the Social Groups*

	Bonobo groups				Chimpanzee groups		
	PL	AP	WU	FR	AM	BU	ED
Adult Male	2 (a:1)	4 (a:1, c:1)	3	2 (a:1)	3 (a:1)	4 (c:1)	3
Adult Female	4 (a:1, c:1)	4 (a:2)	2	4	11 (a:1, c:2)	17	4
Adolescent Male	1	–	1 (e:1)	–	1 (e:1)	2	2 (e:1)
Adolescent Female	2 (c:1, d:1)	1 (e:1)	–	1 (c:1)	–	5	1
Juvenile/infant Male	1	1 (a:1)	1 (a:1, b:1)	1 (b:1)	4 (b:2)	3 (a: 2, b: 2)	3 (e:1)
Juvenile/infant Female	1	2	1	3 (e:2)	3 (e:2)	7 (a:2, e:1)	–

PL, Wild Animal Park Planckendael; AP, Primate Park Apenheul; WU, Wuppertal Zoo; FR, Frankfurt Zoo; AM, Animal Park Amersfoort; BU, Burgers' Zoo; ED, Edinburgh Zoo.
*a, died during study; b, born during study; c, transfer out of group during study; d, transfer into group during study; e, changed to a higher age class during study.

6. Restraining: the number of attempts by the infant to break contact that were prevented by the mother, divided by the total number of contacts broken by the infant [Hemelrijk & Kogel, 1989].

7. Rejecting: contacts attempted by the infant that were prevented by the mother, divided by the total number of contacts made by the infant [Hemelrijk & Kogel, 1989; Nash, 1978; Locke-Haydon & Chalmers, 1983; Stevenson-Hinde et al., 1980].

8. Grooming: the percentage of contact time spent by the mother on grooming her infant.

9. Nipple-rejecting: frequency of breaking or preventing nipple contact by the mother relative to the total number of attempts to get on the nipple.

Analyses

The nine variables were normalized using log, LN, or arcsine transformations to meet the requirements of parametric testing [Sokal & Rohlf, 1981]. We used factor analysis, with varimax rotation, to interpret the components revealed by principal-component analysis and to calculate factor loadings. The Kaiser-Guttman "eigenvalues greater than one" rule was applied to extract the number of factors. Factor scores were computed for each case. We performed analyses of covariance (ANCOVAs) with a repeated-measures design to assess whether bonobos and chimpanzees scored differently on each factor. Not all mothers contributed equally to the data set, and infants were sampled at different ages. Hence, taking into account the dependency of the data, we opted for a random model. The additional Kenwardroger option [Verbeke & Molenberghs, 1997] specified the appropriate denominator degrees of freedom [Schaalje et al., 2001]. Infant age and maternal age were included as covariates, and infant sex was also incorporated in the model to account for possible sex differences. Tests were performed in STATISTICA (version 5.0) and SAS (release 8.01). We conducted two-tailed tests and set alpha levels at 0.05.

TABLE III. Number of Factors Retained by Factor Analysis With "Eigenvalues Greater Than" One Rule for the Combined Data Set of Bonobos (Pan paniscus) and Chimpanzee (Pan troglodytes)*

Factor	Eigenvalue	% total variance
1	2.15	23.91
2	1.68	18.70
3	1.58	17.59
Cumulative %		60.19

*% of variance explained by each factor and in total is indicated.

TABLE IV. Factor Loadings: Matrix of Correlation Between Maternal Behaviors and the Two Factors Extracted by Factorial Analysis for the Combined Data Set of Bonobos (Pan paniscus) and Chimpanzees (Pan troglodytes)*

Maternal behavior	Protectiveness	Distance	Refuse
Making contact	**0.83**	0.23	−0.06
Breaking contact	0.06	**0.83**	0.20
Approaching	**0.70**	0.27	−0.19
Leaving	0.06	**0.77**	−0.20
Grooming	−0.34	0.22	−0.42
Rejecting	−0.06	0.36	**0.78**
Restraining	**0.60**	−0.03	0.39
Nipple Rejecting	−0.06	−0.14	**0.76**
Ventral contact	**0.63**	−0.33	0.04

*The coefficients in each column (factor loadings) indicate how much weight is assigned to each factor. Factors with large coefficients (larger than 0.5 are in bold) for a variable are closely related to that variable.

RESULTS

The factor analysis extracted three significant components from the nine variables of maternal behavior (Table III). The factor loadings are included in Table IV. The factor analysis retained 60.19% of the total variance.

Factor 1 accounted for 23.91% of the total variance. This factor can be defined as "protectiveness," since it correlated positively with making contact, approaching, restraining, and ventral contact. Factor 2 accounted for 18.70% of the total variance. This factor correlated positively with contact-breaking and leaving. We will refer to this factor as "distance." The third factor accounted for 17.59% of the total variance, and correlated positively with rejecting and nipple-rejecting. We will refer to this factor as "refusal."

We computed factorial scores for each case for each factor, and plotted them against infant age (see Figs. 1–3).

In the next step, we conducted three ANCOVAs to investigate whether interspecific differences are apparent in the factor scores of protectiveness, distance, and refusal.

The ANCOVA on the protectiveness factor revealed a general effect of infant age: protectiveness was negatively related with infant age ($F_{1,26} = 50.32$, $P < 0.0001$), but no species difference was found ($F_{1,12} = 0.71$, NS) (Fig. 1). On average, the bonobos and chimpanzees had the same protectiveness factor scores (0.09 ± 0.23 and -0.18 ± 0.23, respectively).

However, the analysis for the second factor, distance, resulted in a significant species × infant age interaction effect ($F_{1,68} = 14.72$, $P < 0.001$) (Fig. 2). The
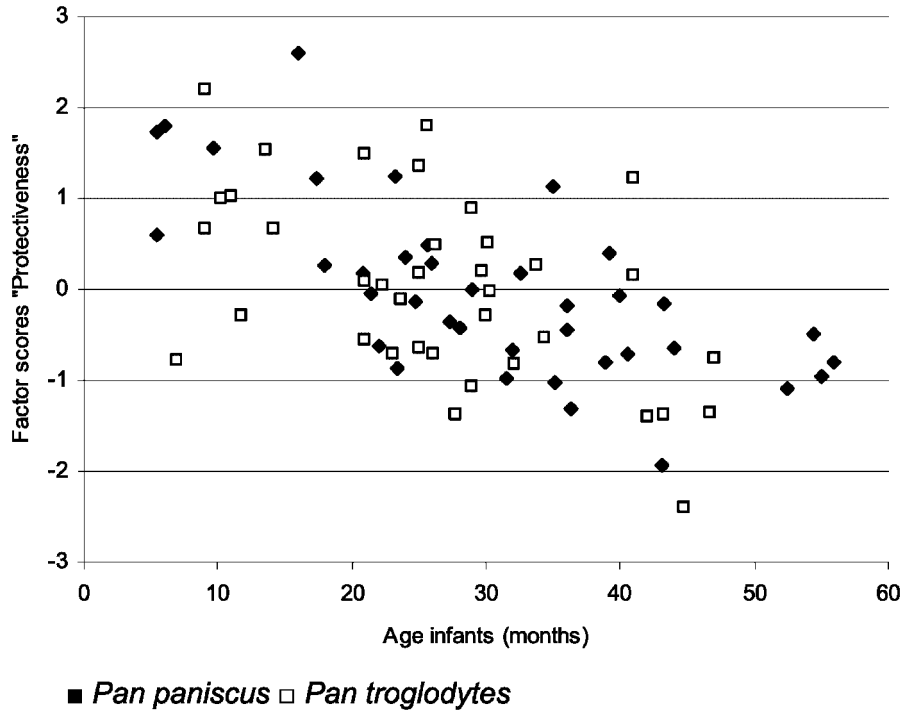
Fig. 1. Factor scores for the protectiveness factor according to infant age for bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*).

factor scores on distance followed a negative relationship with infant age in bonobos ($F_{1,13} = 4.72$, $P < 0.05$; intercept=1.22, slope=−0.03), and a positive relationship with infant age in chimpanzees ($F_{1,32=}8.01$, $P < 0.01$; intercept=0.92, slope=0.03).

A general species effect was found when we compared the factor scores on refusal ($F_{1,12=}7.50$, $P = 0.01$). On average, bonobo females had higher refusal scores than chimpanzee females (0.59 ± 0.28 and -0.47 ± 0.28, respectively; Fig. 3).

DISCUSSION

The aim of this study was threefold. First, we investigated whether a factor analysis used to determine maternal styles in *Cercopithecine* species could be applied to bonobos and chimpanzees in captivity. Second, we sought to determine whether they follow the same pattern. Third, we assessed whether a species effect on maternal style is apparent.

The results of the factor analysis for the *Pan* species show certain similarities but also differences in comparison with the pattern usually found in *Cercopithecine* species [Bardi & Huffman, 2002; Fairbanks, 1996; Fairbanks & McGuire, 1988]. The total variance retained by the factor analysis is comparable with previous results from *Cercopithecine* species [Bardi et al., 2001; Bardi & Huffman, 2002]. However, our analysis reveals three factors: one protective factor (protectiveness) with high positive loadings on making contact, approaching,
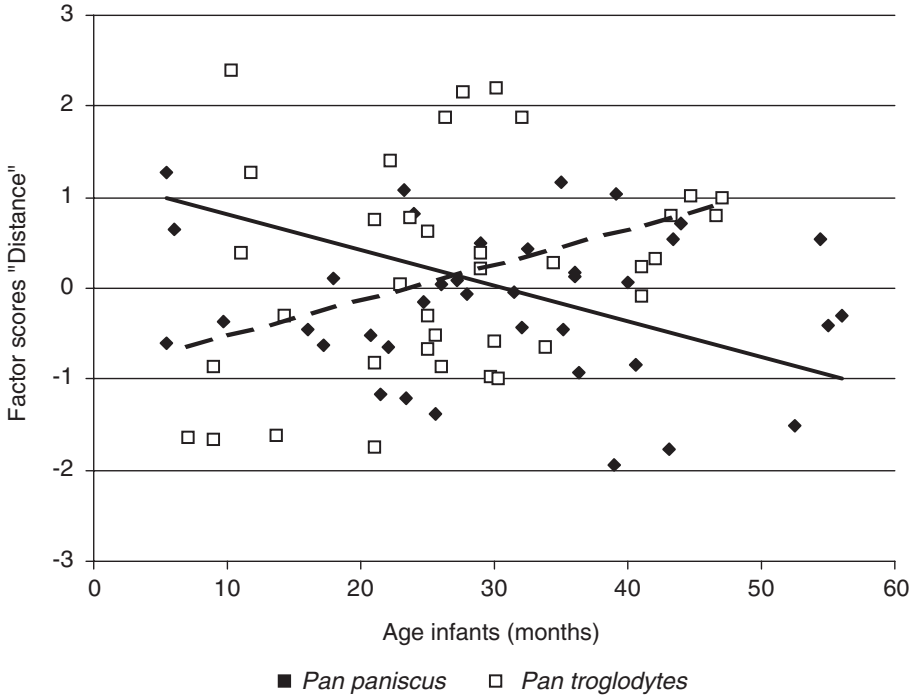
Fig. 2. Factor scores for the distance factor according to infant age for bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*).

restraining, and time in ventral contact; and two rather rejecting factors–the first (distance) with high positive loadings on breaking contact and leaving, and the second (refusal) with high positive loadings on rejecting and nipple-rejecting. The first factor pattern corresponds with the pattern found in *Cercopithecine* species, which seems at least to confirm a high degree of consistency of the protectiveness dimension across species and higher taxa. While in *Cercopithecine* species the rejection factor has generally high loadings on breaking contact, leaving, and rejecting, this factor appears to be divided into two factors in the *Pan* species. A possible explanation may be that we treated rejecting and nipple-rejecting separately. The term ''rejecting'' is not always uniformly defined in the *Cercopithecine* literature. Sometimes it includes both nipple and contact rejection [Fairbanks & McGuire, 1988], and sometimes only the latter is used [Bardi et al., 2001; Bardi & Huffman, 2002]. Given that rejecting and nipple-rejecting may be more related to regulation of nipple contact or nursing than to bodily contact per se, we chose to treat them separately. Our results now indicate that in the *Pan* species, breaking contact and leaving an infant (maternal behaviors related to promoting distance with the infant) represent another dimension of maternal style in addition to rejecting and nipple-rejecting.

The third aim of this study was to assess whether a species effect on the maternal style is apparent. The ANCOVA on the factor scores for the protectiveness factor revealed no species difference for protectiveness, but species differences were found for both the distance and refusal factors. Hence, our results indicate that there is a species effect on maternal style.
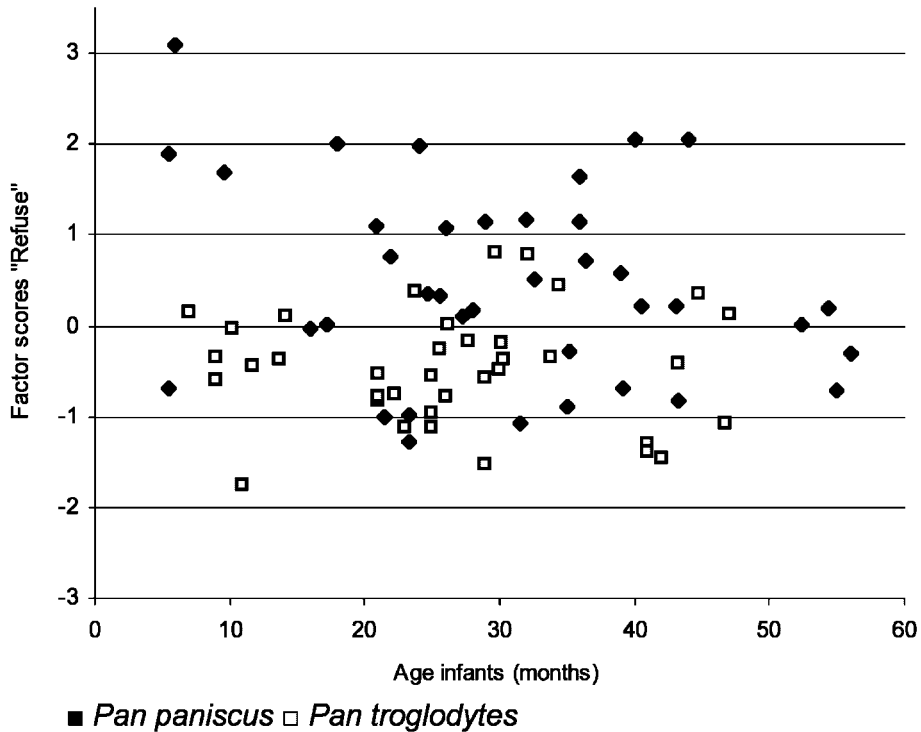
Fig. 3. Factor scores for the refusal factor according to infant age for bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*).

Maestripieri [1994b] argued that in stumptail macaques (*Macaca arctoides*), "the relaxed and detached mothering style of stumptail mothers is in tune with the benign nature of interactions between their infants and other group members" and "the higher control and protectiveness of rhesus and pigtail mothers fits well with the risk of harrassment and kidnapping associated with infant handling in these species." An interspecific comparison of aggression performed by adults toward infants reveals that chimpanzees generally score slightly higher than bonobos, and the difference becomes more apparent as the infants and juveniles grow older (unpublished data). These data suggest that chimpanzees are less tolerant toward juveniles than are bonobos. Rather than being a real threat, these aggressions may serve a function in the social development of the juveniles. However, mortality rates in captivity indicate that more chimpanzee infants die before the age of 5 than bonobo infants [De Lathouwers & Van Elsacker, in press]. A fraction of the chimpanzee infant deaths in captivity can be attributed to social aggression by adult males and females [Courtenay, 1988; Spijkerman et al., 1990], and there are indications that infanticide poses a higher risk to chimpanzees than bonobos [Doran et al., 2002; Wrangham, 2000, 2002]. Nevertheless, given the low frequency of infanticide, the trade-off between higher maternal protectiveness and reproductive output may be too low. A comparison of reproductive parameters between bonobos and chimpanzee in captivity reveals that chimpanzee mothers appear to compensate for a higher infant mortality rate with a higher fertility rate [De Lathouwers & Van Elsacker, in press].

More detailed data on cause of infant death may provide valuable information in order to conclude whether or not threats to infant survival are comparable between species, and whether higher maternal protectiveness may or may not protect infants from these mortality causes.

We did find a species difference concerning the promotion of distance. Whereas bonobo females are initially more inclined to more frequently break contact with their infants and leave their infants more frequently when their infants are young, the frequency declines when there infants become older. In chimpanzees we find the reverse pattern: breaking contact and leaving by mothers increases with infant age. Promoting distance is probably related to active stimulation of spatial independence. Chimpanzee infants are known to spend more time more than five meters away from their mothers than bonobo infants, especially from 20 months of age onward [De Lathouwers, 2004, Ph.D. dissertation). This coincides with the point at which the regression lines between distance and infant age (see Fig. 2) of each species cross. By the time their infants are 20 months old, chimpanzee mothers start to score higher on the distance factor than bonobo mothers. Hence, the promotion of distance by chimpanzee mothers seems indeed related to the development of the spatial independence of their infants. The initial lower frequencies of contact breaking and leaving in chimpanzees may be attributed to higher risk of infanticide of young infants in chimpanzees, as already mentioned before. The development of spatial independence of bonobos evolves more slowly (De Lathouwers, 2004, Ph.D. dissertation), and appears to be related to a lower intention of bonobo mothers to actively promote distance with their infants by means of breaking contact and leaving. Although these arguments suggest plausible explanations for the differences found, the overlap of the distance factor scores between bonobos and chimpanzees is considerable. Therefore our explanations are tentative and further investigation, preferably with a larger sample size and a larger time window on infant development, are recommended in order to make more general conclusions.

The higher refusal scores for bonobo females are likely related to the regulation of nursing. The frequency of nursing, the duration of the nursing bouts, and the intensity of the suckling stimulus are known to be related to the length of postpartum amenorrhea [McNeilly, 1988; McNeilly et al., 1988]. The higher refusal by bonobo females appears to control the frequency and duration of nursing bouts (the average frequency of nursing bouts per 30 min is higher, and the average duration of a bout tends to be shorter in bonobos than in chimpanzees [De Lathouwers, 2004, Ph.D. dissertation]). Although wild bonobo females are known to resume estrus within a year of giving birth [Kano, 1992], this does not automatically imply that they immediately begin to ovulate and are able to conceive [Furuichi & Hashimoto, 2002]. We have no endocrinological data or data on resumption of estrus for all of the females in our data set with which to test this hypothesis. However, more indirect evidence of later resumption of ovulation may come from the length of the interbirth interval, which is known to be longer in captive bonobos than in chimpanzees (De Lathouwers and Van Elsacker, in press). Hence, there are indications that bonobo females may more actively regulate infant nursing, probably in order to regulate postpartum ovulation and the length of the interbirth interval. Endocrinological data would be very valuable in further clarifying this issue. Another explanation for the higher rejection and nipple rejection scores of bonobos may be that bonobo mothers restrict nursing to times when it does not hinder other activies (e.g., social activities). Bonobo mothers in general are more social than chimpanzee mothers [Doran et al., 2002; White, 1996]. Wild chimpanzee females spend the majority of their time alone or

with only their family [Goodall, 1986; Wrangham & Smuts, 1980], although great variability between chimpanzee sites occurs [Boesch & Boesch-Achermann, 2000]. Unfortunately, detailed interspecific comparisons of female sociality in captivity are not available. However, if bonobo females are indeed more social, they may have less time to be actively occupied with their infants compared to chimpanzee mothers, or they may need to restrict mother–infant social interactions to times that are more convenient for them.

In conclusion, our study indicates that it is feasible to use a factor analysis to determine maternal style in the *Pan* species. The results do not totally correspond with the pattern usually found in *Cercopithecine* species, which may be partially due to slight differences in maternal-behavioral definitions of rejecting and nipple-rejecting. Species differences between bonobos and chimpanzees were found in two of the three dimensions of maternal behavior. These differences in maternal styles apparently are related to interspecies differences in infant development, infant vulnerability to aggression, interbirth intervals, and female sociality. Although the interspecies differences in maternal style appear to be adaptive, further investigation is recommended to test in greater detail the explanations brought forward in this study. There are indications that captivity influences the reproductive performances of bonobos and chimpanzees differently [De Lathouwers & Van Elsacker, in press]. One example is the fact that in the wild, the interbirth interval tends to be shorter in bonobos than in chimpanzees [Furuichi et al., 1998], while the reverse is found in captivity [De Lathouwers & Van Elsacker, in press]. It is therefore not unlikely that maternal behaviors are likewise affected, and one should keep this in mind when comparing these results with in situ findings.

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